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SHORT COMMUNICATION

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Abstract

Ant nests are relatively stable and long-lasting microhabitats that attract a diverse group of arthropods. Particular stressors, however, can trigger ants to relocate their nest to a new site. It is unclear how associated arthropods respond to occasional nest moving of their host. Here, I report field observations which showed that the potentially parasitic larvae of the beetle *Clytra quadripunctata* follow their red wood ant host during nest relocation, either by crawling on their own or by being carried by the host workers. These observations shed new light on the spatial dynamics between ants and their associates.

Introduction

The large group of arthropods that live as guests in the nests of social insects disperse in a metapopulation context from one suitable host nest to another. Dispersal involves the successful detection and tracking of their host nest in the landscape, presumably following host-specific chemical cues (Akre and Rettenmeyer 1968; Hölldobler 1970). The host might periodically move to new nest sites (McGlynn 2012). Many associated guests freely walk or crawl in the nest and feed on brood or pilfer retrieved prey. Nest relocation by the host will force these associates to decide whether to follow the host to a new site or to stay in the abandoned nest. Following the host will ensure a continuity of food and protection for the guest, but requires specific adaptations to recognize the onset of nest relocation and to track the new nest. Successful host following has been widely reported in arthropods associated with nomadic army ants. Army ant guests can detect the pheromone trails of their host and are well known to run among the moving horde (Akre and Rettenmeyer 1968; Hölldobler and Wilson 1990). However, behaviour of their host ants is highly atypical for social insects, as they do not construct permanent nests and almost continuously migrate to new temporary nest sites. Consequently, associates of these itinerant hosts evolved advanced tracking behaviour to be able to keep up. In contrast, social insects with permanent nests only move occasionally and how guests respond to the infrequent and unpredictable nest relocation events is poorly studied. So far, it has been anecdotally reported that the rove beetle *Dinarda* and the sowbug *Platyarthrus hoffmannseggii* followed their *Formica* host to a new nest site (Wheeler 1910; Donisthorpe 1927).

European red wood ants construct large conspicuous nests with an aboveground mound of organic thatch. They can occupy a nest site for many years and even decades (Gösswald 1989).

Nevertheless, when nest conditions start to deteriorate, red wood ants are capable of moving the entire colony to new nest sites (Möglich and Hölldobler 1974). Their nests harbour a rich community of obligately associated arthropods (Parmentier et al. 2014). The larvae of the leaf beetle (Chrysomelidae) *Clytra quadripunctata* (Linnaeus, 1758) are common members of this nest-inhabiting community (Parmentier et al 2015). They are protected by a hard, pear-shaped case made of excrements and nest material (Fig. 1). Lab tests demonstrated that their larvae preferentially live in the dense brood chambers of red wood ants (Parmentier et al. 2016a). This is confirmed by observations in the field, where I mostly detect the larvae in the deep and thermoregulated brood chambers. The exact effect of these larvae on their host is not fully understood. Lab tests showed that they readily feed on ant brood and prey collected by the ants (Parmentier et al. 2016b). It was also argued that they consume organic nest material and debris (Donisthorpe 1902). Their isotopic ^{15}N enrichment, which was considerably higher than expected for a strict decomposer (Parmentier et al. 2016b), and their preferred position in the brood chambers, however, suggest that they are scavengers with a potential negative effect on their host. Adult beetles hatch from the case and readily escape out of the nest (Fig. 1A). The adult beetles settle and feed on plants near wood ant nests. After mating, the female deposits her eggs covered with a protective case of excrements near or on the nest (Donisthorpe 1902). It has been suggested that the beetle eggs are picked up by the ant workers and carried into the nest (Donisthorpe 1902). But possibly, the hatched larvae can locate neighbouring nests and colonize them on their own. Here I report how the larvae adaptively respond to an occasional nest relocation event of its red wood ant host.

Methods

On 02.05.2018 I observed a colony of the red wood ant *Formica polyctena* Förster, 1850 relocating its nest in the nature reserve Hoge Dijken in Oudenburg, Belgium. Colony relocation in red wood ants can be recognized by massive amounts of workers carrying brood and other adults (social carrying) in a stereotyped way to another nest site (Möglich and Hölldobler 1974) (Fig. 1B, video S1). The new nest site was 5 meters away from the old nest and was constructed on top of a large pile of woodchips originating from chopped exotic trees growing in the reserve (Fig. 2). A closer look at the emigration column, revealed the presence of crawling larvae of *Clytra quadripunctata*. The old nest was large (surface area 0.87 m^2) and very active at least until the beginning of April 2018 (last visit to this site prior to the nest relocation). It has been lying there for minimum 12 years (pers. communication Dr. W. Dekoninck). The organic mound was constructed on a fallen tree branch. When I observed the emigration column on 02.05.2018, the organic mound was disintegrated and the tree branch was exposed. The nest was no longer repaired and material of the original mound was brought to the new nest. Probably the peak of nest moving was already going on for some days, and the first relocations may already started weeks before (cf. Mabelis 1978). I returned to the study site to observe the progress of the nest relocation and its effect on the behaviour of *C. quadripunctata* on 04.05.2018 and 11.05.2018.

On 08.08.2018, I tested the behaviour of red wood ants towards the larvae of *C. quadripunctata* by placing twenty beetle larvae at the foot of the wood chip pile (50 cm from nest entrance on the pile) within a very active ant trail.

Results and Discussion

I here report a rare observation of an intranidal ant associate or myrmecophile joining the host colony relocation to a new permanent nest site. I observed that the larvae of the beetle *Clytra quadripunctata* accompanied their red wood ant host *Formica polyctena* to a new nest site. Most of the beetle larvae crawled to the new nest on their own during nest relocation. Some, however, were also carried over a short distance by a host worker.

On 02.05.2018, I detected 45 *C. quadripunctata* larvae which were slowly crawling in company with a moving *F. polyctena* colony towards a new nest site. (Fig. 1B-D, Fig. 2, video S1, Table 1). None of the larvae headed back to the old nest. I also observed 135 beetle larvae crawling to the top of a pile of wood chips, where the new nest was founded (Fig. 2). I found 21 *C. quadripunctata* larvae on the top of the old nest and in a cavity of a tree branch that supported this nest. Two days later, the emigration was still ongoing, but considerably less intense. Now I only detected two immobile larvae in the emigration column, 51 larvae on the pile and 17 larvae on the old nest. I also observed winged sexuals on the new nest. On 11.05.2018, the old nest was completely deserted, but I still found 15 larvae on top and in the branch. No larvae were seen between the nests. In addition, I did not find any larvae on the new nest (Table 1). As the larvae mostly reside in the deep parts of the nest (Parmentier 2016 et al. a, pers. observations), they probably moved to the core of the new nest. This was confirmed by turning a wood piece on top of the new nest, where I found three larvae.

Remarkably, I also saw three different beetle larvae picked up and dragged by the ants in the direction of the new site (Fig. 1D and 1E, video S2) on 02.05.2018. Ants, however, did only transport the larvae during a part of the trajectory between the nests. The transport of the heavy larvae was hampered by obstacles along the trajectory. When the larvae got stuck, they were dropped. In one occasion, I saw another worker picking up a dropped beetle larvae and

transporting it for some metres. The attractiveness of the larvae to the ants was further underlined with a small experiment on 08.08.2018. Twenty beetle larvae were placed at the foot of the wood chip pile (50 cm from nest entrance on the pile) within a very active ant trail (position indicated with B on Fig. 2). Thirty minutes later, six larvae were carried by the workers to the top of the pile where the new nest was constructed, four larvae were transported over a distance of circa 15 cm to the nest, two larvae were dragged for some centimetres and eight larvae were ignored. Carrying of the covered eggs and larvae was already described in the beginning of the 20th century (Donisthorpe 1902). The case or the larvae could release appeasing substances, a strategy used by other associates that are carried by their ant host (Hölldobler and Wilson 1990; Witte et al. 2002). Alternatively, the ants might mistake the case for building material, which is constantly brought to the nest.

Accompanying the host to the new nest is an adaptive response, as the beetle will secure its food provisioning and protection. The beetle larvae are always found in red wood ant nests and are probably not able to survive in isolation of its host (Donisthorpe 1902). Nest relocations in social insects mainly occur in response to shifts in microclimatic conditions or after a sudden disturbance (McGlynn 2012). In other animal groups such as mammals (Lewis 1995) and birds (Goguen and Mathews 1996), parasite avoidance has been argued as alternative major driver for nest relocation. So far, parasitic load as a trigger for nest relocation was only demonstrated in one eusocial insect, i.e. the wasp species *Mischocyttarus labiatus* (Litte 1981), but red wood ants may also benefit from avoiding parasites in accordance with the parasitic load hypothesis posed by McGlynn *et al.* (2004). I found that a large fraction of the potential harmful beetle larvae stayed behind in the old nest (Table 1). Red wood ant nests also harbour many other brood predators and cleptoparasites (Parmentier et al. 2014, 2016b) and likely a significant part will not be able to find the new nest site. Consequently by moving to a new site, red wood ants

may considerably reduce parasite load. The new nest is only 5 metres away, but relocations to more remote sites may reduce parasite load even further.

Tables

Table 1.

date	Larvae in old nest (*N*)	Larva crawling between nests (*N*)	Larvae carried (*N*)	Larvae on pile and new nest (*N*)
02.05.2018	21	45	3	135
04.05.2018	17	0 (2 immobile)	0	51
11.05.2018	15	0	0	0

Supplementary material

Video S1: A crawling *Clytra quadripunctata* larva following the host ant migration column to the new nest. Note the transport of adult workers (social carrying) in the ant column, typical behaviour displayed during ant nest relocation.

Video S2: *Clytra quadripunctata* carried by the host ant *Formica polyctena*.

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Figures

Fig. 1. *Clytra quadripunctata* and its host *Formica polyctena.* A) A red wood ant worker is inspecting an adult of *C. quadripunctata* which resides on plants near the nest of its host ant. B) A beetle larva crawling on its own to the new nest. A worker is transporting another worker in the background (indicated with arrow). The transported worker folds its legs to the body and bends its abdomen. This adult transport (social carrying) is typical observed during nest relocation (see also video S1). C) A larva of *Clytra quadripunctata* is accompanying the migration column of its host ant *Formica polyctena* during nest relocation. D) The beetle larva can protect its soft white body by sealing the case with its armoured head (brown). Workers on the bottom of the figure are inspecting another beetle larva during the nest relocation. E) A worker is carrying a beetle larva during nest relocation (see also video S2).

Fig. 2. Positioning of the old and new nest. The new nest covered with fine thatch lies on top (indicated with an ellipse) of a pile of woodchips. Crawling larvae between the nest and transported larvae were observed at the location indicated with A. Larvae were offered at the the foot of the pile, position indicated with B.

Fig. 1

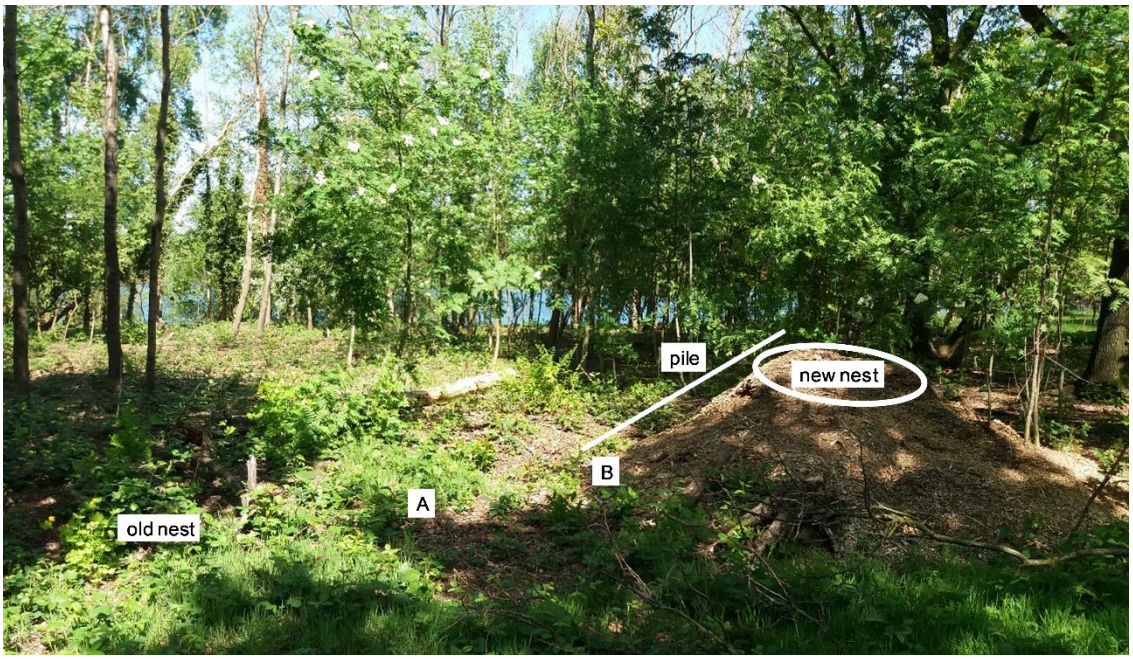

Fig. 2

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